HUMPBACK WHALES *(MEGAPTERA NOVAEANGLIAE)* IN THE WESTERN NORTH ATLANTIC OCEAN

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Individual humpback whales can be recognized by natural markings on their bodies. The North Atlantic Humpback Whale Catalogue contains photographs of the ventral flukes of over 4000 humpback whales. More than a thousand resightings over the past 15 years have yielded information on seasonal distribution, population substructure and abundance. This paper reviews the biology of humpback whales in the North Atlantic Ocean, highlighting contributions made by photo-identification studies, and indicates avenues for future research.

During boreal summer, North Atlantic humpbacks form at least 5 geographically distinct feeding aggregations at latitudes from about 42°–78° N. Known feeding aggregations occur in the Gulf of Maine (c. 400 individuals), Gulf of St. Lawrence (c.200); Newfoundland and Labrador (c.2500); western Greenland (c.350); Iceland-Denmark Strait (up to 2,000); and Norwegian Sea (1000). Photo-identified whales from all feeding aggregations including and to the west of Iceland spend boreal winter near the Virgin Islands, Puerto Rico and the Dominican Republic (c.17°–22°N), where courtship, interbreeding and calving occur. Some of these whales pass close to Bermuda during the northward migration. The winter ground(s) for European humpbacks is not yet known. A variance-weighted estimate for the total population of humpback whales in the North Atlantic Ocean west of Iceland during 1978–1988 is 5066±3266) (95% CI).

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Humpback whales *(Megaptera novaeangliae)* play important roles in the ecology and economy of the North Atlantic Ocean. Here, as in other oceans, they were economically significant to aboriginal people and commercial hunters as a source of meat and oil. Now, the accessibility of their coastal habitats, their willingness to approach boats, and the frequent opportunities they provide for people to watch feeding, breaching or other interesting behaviors have made them the mainstay of whale watching industries along the New England coast and in eastern Canada. Commercial whale watching tours in New England, for example, now take out nearly 1,500,000 people each year, representing over $23,000,000 in ticket sales alone. On the other hand, fishermen along the coast of Newfoundland regard humpbacks as pests, because their frequent entrapment or entanglement in shorefast nets set for salmon, cod or capelin, cause gear damage, loss of fishing time and economic hardship (Lien et al., 1990).

Although the difficulty of estimating prehunting humpback abundance (NMFS, 1990) confounds attempts to evaluate its ecological role in the past, it is certainly important at some locations today. During summer, the species is the major cetacean predator in the southwestern Gulf of Maine and at some locations in the Canadian Maritimes. During winter, humpbacks migrate to warm, low latitude waters where they feed only rarely (Baraff et al., 1991), but where they may be the dominant cetacean in biomass, and their sounds, excretions, or other factors may be of ecological significance (Katona and Whitehead, 1988).

Early descriptions of humpbacks in the North Atlantic came from opportunistic observations at sea or dead animals killed during hunting or found dead along the shore (e.g., True, 1904; Allen, 1916; Ingebritsen, 1929). The comprehensive studies of large samples in the Southern Hemisphere (e.g. Matthews, 1937; Chittleborough, 1958,1965) or the North Pacific (e.g. Nishiwaki, 1959) were not carried out in the North Atlantic, because humpbacks were al-

FIG. 1. Map of North Atlantic Ocean. Modified from Jonsgard (1966).

ready scarce before such studies became routine.

Schevill and Backus's (1960) observation over a 10 day period of a humpback whale swimming near Portland, Maine, was one of the first attempts to study a free-living humpback for purely scientific purposes. Their use of distinctive dorsal fin shape and fluke pigmentation to conclude that the same individual was present on different days may have been the first modern use of the technique that has become a cornerstone of humpback whale research. Examples of the development and use of fluke photographs to identify humpback whales in the North Atlantic and other oceans are contained in Hammond et al. (1990).

METHODS FOR PHOTO IDENTIFICATION OF HUMPBACK WHALES

Pigmentation patterns on the ventral surface of the flukes of humpback whales were photographed, printed in standard format and analyzed as discussed in Katona and Whitehead (1981), Katona and Beard (1990)and Lien and Katona (1990). Approximately 10,000 photographs of the flukes of humpback whales collected by research workers and amateurs throughout the Atlantic region from 1967 to the present are maintained at College of the Atlantic (COA) in Bar Harbor, Maine, as the North Atlantic Humpback Whale Catalogue. Contributors are asked to submit at least one fluke photograph of every individual photographed each season. Each photograph obtained is compared to the entire collection to determine whether it represents a previously known whale or a new whale. Photographs of the same individuals taken at different times and places are used to study long distance migrations, population subdivisions, and to estimate population abundance using capture-recapture techniques (Hammond, 1986). Updated sightings data from the COA catalogue are provided periodically to contributors of photographs, some of whom maintain regional photographic collections containing detailed sighting records for individual whales in localized study areas that are used, for example, to chart reproductive histories of individual females (Clapham and Mayo, 1987a,b; 1990), or investigate social behavior (Weinrich and Kuhlberg, in press).

HUMPBACK WHALES IN THE NORTH ATLANTIC OCEAN

A. Distribution and Feeding on the Summer Range

During summer, humpback whales feed over the continental shelf and along coastlines from the British Isles north to Bear Island (75°N) and Spitsbergen (78°N), and around Iceland, southwestern Greenland, Newfoundland and Labrador, the Gulf of St. Lawrence, and the Gulf of Maine (Tomilin, 1967; Leatherwood et al., 1976; Whitehead et al., 1982; Mitchell and Reeves, 1983; Katona et al., 1983; Perkins et al., 1984, 1985; Payne et al., 1986; Whitehead, 1987).

This distribution was documented relatively early from locations of whaling catches, but previous investigators (e.g. Kellogg, 1929; Mitchell, 1974) had little or no information about movements between those regions and no effective method for obtaining more. About 15 years ago, the questions raised by those authors began to be answered by charting the movements of photographically-identified humpbacks.

Our conclusions regarding migrations, population subdivisions and abundance of humpback whales in the North Atlantic Ocean are drawn from the study of 10,566 photographs, represesenting 4,021 individual whales. By December, 1988, 1,428 individual whales had been seen on more than one day (a total of 4,012 sightings) and 1,083 individuals had been seen in more than one season or in different geographic regions (a total of 3,173 sightings). Photographs from field seasons subsequent to 1988 are still being analyzed.

Geographic patterns of resightings on the summer range (Fig. 2) suggest that during summer the population of humpback whales from Iceland westward is divided into several relatively distinct units. Individually-identified whales from Iceland, southwestern Greenland, Newfoundland and Labrador, the Gulf of St. Lawrence, or the Gulf of Maine returned repeatedly to those same waters. We use the term "feeding aggregations" to describe the groups of whales using those separate parts of the feeding

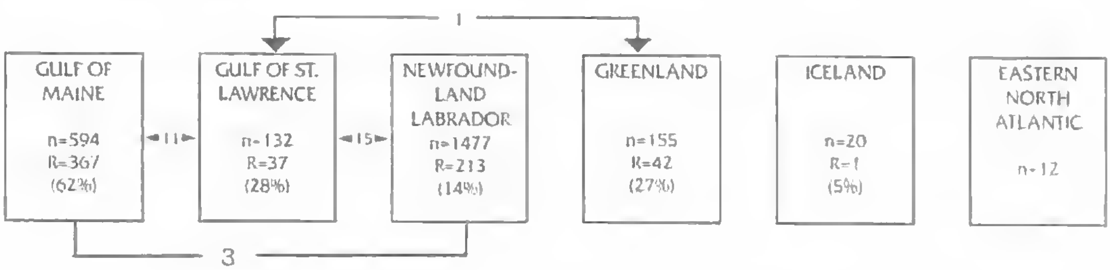

FIG. 2. Movements of photographically identified Humpback Whales on the North Atlantic summer range. Boxes represent regional feeding aggregations. Number of individuals photographed (n); number resighted in a region in different years (R); and percentage resighted in the region in different years are shown. Numbers of individuals photographed in more than one region are shown between boxes.

LOCATION	PREY SPECIES	SOURCES
Iceland	capelin (*Mallotus villotus*),herring (*Clupea harengus*)	
Greenland	small fish, krill, sand lance (*Ammodytes* sp.)	Kapel,1979; Perkins et al.,1982
Newfoundland	capelin (*Mallotus villosus*), euphausiids, haddock, (*Melanogrammus aeglefinus*), mackerel (*Scomber scombrus*), sand lance (*Ammodytes* spp.), squid (*Illex illecebrosus*)	Mitchell,1974; Bredin,1983; Whitehead and Glass, 1985; Whitehead and Carscadden,1985
Gulf of St. Lawrence	herring (*Clupea harengus*), capelin (*Mallotus villosus*), sand lance (*Ammodytes* sp.), euphausiids	R. Sears pers. comm.
Nova Scotia	herring (*Clupea harengus*), krill (*Meganyctiphanes norvegica*)	Brodie et al.,1978; C. Haycock pers. comm., S. Katona unpubl. data
east coast USA	sand lance (*Ammodytes* sp.), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), krill (*Meganyctiphanes norvegica*)	Meyer et al.,1979; Overholts and Nicolas, 1979; Watkins and Schevill,1979; Hain et al.,1982; Katona et al.,1983; Kenney,1984; Hays et al.,1985; Kenney et al.,1985, Kenney and Winn,1987; Winn et al.,1987; Mayo et al.,1988; Geraci et al., 1989

TABLE 1. Prey species utilized by humpback whales in the North Atlantic Ocean

range. Little interchange was seen between feeding aggregations (Fig. 2). In some cases, interchange shown between regions may be animals that happened to be seen while enroute to their feeding destination. For example, the three individuals photographed in both the Gulf of Maine and Newfoundland may have used the Gulf of Maine only for migration, since they were observed there at the very beginning and very end of the feeding season. Interchange between the feeding aggregation in the Gulf of St. Lawrence and those in Newfoundland (including Labrador) or the Gulf of Maine is relatively large because of their proximity. Individuals bound for the Gulf of St. Lawrence probably swim through waters used by other feeding aggregations.

Photo-identification studies from the eastern North Atlantic Ocean are planned or in progress, but not enough data are yet available for comparable analysis. No resightings were found of 12 individuals from the eastern Atlantic represented in the COA collection.

Distribution on the summer range is directly dependent on the distribution and abundance of prey. However, since humpbacks in the North Atlantic utilize several types of prey (Table 1), the pattern is somewhat more complex than in the Antarctic, where krill, primarily *Euphausia superba*, dominates the diet (Matthews, 1937; Laws, 1985). In the western North Atlantic, humpbacks arrive by mid-April at the Massachussetts coast, the portion of the feeding range closest to the winter range. In more northerly areas they usually appear by May or early June, with peak numbers in July or August. Typical annual movements within a feeding region are keyed to annual cycles of prey abundance. For example, the intensive whalewatching industry operating from mid-April to mid-October along the Massachusetts coast exists because many whales remain in that region throughout summer, feeding mainly on a population of sand lance resident at Stellwagen Bank (Mayo et al., 1988). In contrast, humpbacks migrate steadily along the coast of Newfoundland following the northward progression of capelin spawning from June through October (Whitehead et al., 1982).

Feeding areas have changed substantially between weeks or years depending on local abundance and distribution of prey (see Table 1).

No strong evidence of age or sex class segregation has been found on the summer range. For example, in continental shelf waters of the U.S., the geographic distribution of mothers with calves and of juveniles is similar to that of other humpbacks (Goodale, 1982).

By late autumn, most humpbacks begin migrating to lower latitudes. However, winter records from Newfoundland (Williamson, 1961; Jon Lien, pers. comm.), the Gulf of Maine (CETAP, 1982; Mayo et al., 1988; C. Haycock, pers. comm.) and northern Norway (Rister, 1912, cited in Kellogg, 1929) indicate that some whales may stay at high latitudes all winter.

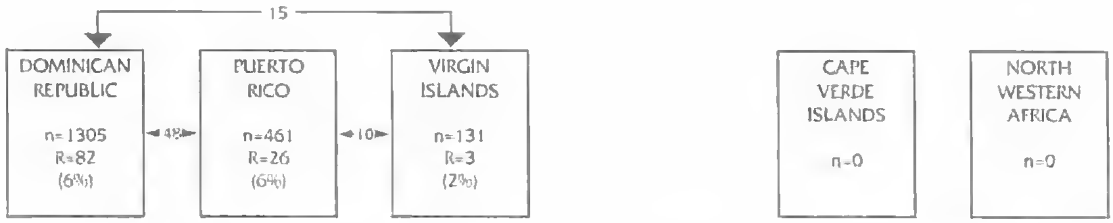

FIG. 3. Movements of photographically identified humpback whales on the West Indies winter range. Number of whales photographed (n) is shown for each breeding location, along with number (R) and percentage of whales photographed at that location during different winters. The number of whales photographed in more than one location is also shown.

Events observed during late November in the southwestern Gulf of Maine, preceeding migration to the West Indies winter range, include increased numbers of whales, energetic swimming behavior and song production (Mattila et al., 1987).

Migration routes of different feeding aggregations between the summer range and the winter range are not known. Humpback whales probably migrate well offshore to their principal winter range around the Greater and Lesser Antilles, since no winter sightings have been recorded along the U.S. coast or at Bermuda. Songs of humpback whales enroute to the winter range were heard on underwater sound recordings made east and south of Bermuda and also southwest of there (Clapham and Mattila, 1990).

B. Distribution on the Winter Range

From late December through early April, most of the western North Atlantic humpback population is found at Silver Bank and Navidad Bank, reefs approximately 607 nm^2 and 157 nm^2, respectively, located about 120 km north and northwest of Puerto Plata, Dominican Republic. At least 2000 humpbacks occur there from December to early March (Balcomb and Nichols, 1978,1982; Whitehead and Moore, 1982). Winn et al. (1975) estimated that 85% of the entire western North Atlantic breeding population used Silver and Navidad Banks. Significant numbers of humpback whales also winter along the Dominican coast (Mattila et al., 1988), the northwest coast of Puerto Rico (Winn et al., 1975; Mattila, 1983) and on the Virgin Bank (Winn and Winn, 1978; Mattila and Clapham, 1989). Movement of whales between those portions of the winter range occurs within a season and between years (Fig. 3). The remainder of the population may be scattered throughout the Lesser Antilles as far as Venezuela (Winn and Winn, 1978).

The wintering grounds of eastern Atlantic humpbacks have not yet been documented by either recovery of artificial tags or photo-identification studies. Humpbacks were killed by hunters during winter around the Cape Verde Islands (Kellogg, 1928; Townsend, 1935; Mitchell and Reeves, 1983) and along the coast of northwestern Africa (Kellogg, 1928). Kellogg's (1928) map of humpback migrations showed all eastern North Atlantic humpbacks using those winter grounds, but the possibility that some eastern Atlantic humpbacks winter around the Antilles can not be ruled out. The Cape Verdes are now being surveyed using photo-identification techniques (F. Wenzel, pers. comm.).

Courtship (Tyack and Whitehead, 1983), singing (Winn et al., 1981; Payne and Guinee, 1983; Payne and Payne, 1985), newborn calves and nursing (Mattila and Clapham, 1989) have all been observed on the winter range. Copulation, which has never been documented in this species, is also presumed to take place there. Differential habitat use by reproductive class occurs on the West Indies winter range. Calm waters around coral heads and reefs providing lee from the trade winds are used preferentially by females with calves (Whitehead and Moore, 1982; Goodale, 1982). Singing males may prefer locations with flat bottoms (Whitehead and Moore, 1982).

Migrations to or from the West Indies winter range have been documented for 339 photographically-identified humpbacks from all feeding aggregations from Iceland west (Fig. 4). Photo-identification has also shown that surface-active courtship groups contain whales from different feeding aggregations (Mattila et al.,

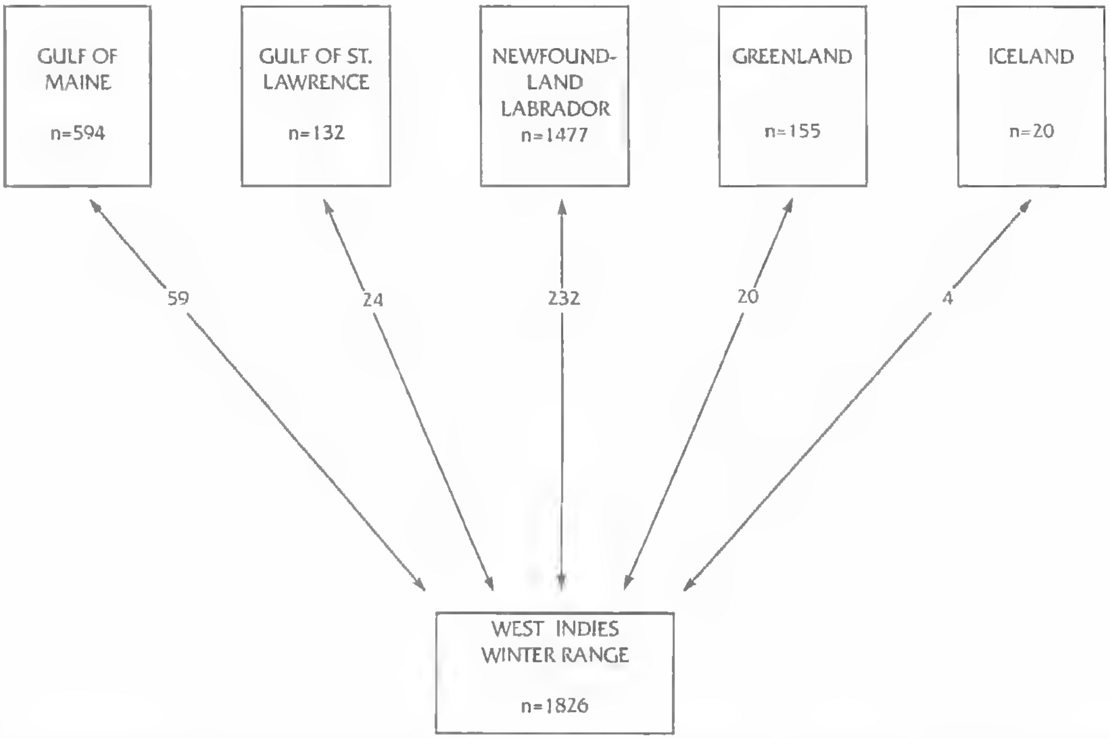

FIG. 4. Migrations between eastern North Atlantic summer range feeding aggregations and West Indies winter range. Number of individuals (n) photographed at different locations is shown along with the number photographed in different locations (on interconnecting lines).

1989), indicating that all humpbacks from the western North Atlantic, at least, probably interbreed.

Some humpbacks remain in the West Indies through March, but most depart earlier. Peak numbers at Silver Bank occured in February (Balcomb and Nichols, 1982). Photo-identified individuals (n=26) from all five western Atlantic feeding aggregations have been observed during northward migration near Bermuda in April and early May (Stone et al., 1987) (Fig. 5), but some whales probably take a a mid-ocean route to the summer range. Minimum mean swimming speeds of 3.29 km/hr (2,684 km in 34 days) and 2.28 km/hr (2,351 km in 43 days) were computed for two photographically-identified whales migrating from the West Indies to the Gulf of Maine feeding aggregation (Clapham and Mattila, 1988). The slower rate was close to mean speeds calculated by Dawbin (1966).

If all western North Atlantic humpbacks interbreed, as suggested by Mattila et al. (1989), and since a calf must nurse during its first migration to the summer range, persistent subdivision of the population on the summer range must be maternally directed. Such divisions probably are caused by the tendency of a calf to return to the portion of the summer range used by its mother and learned during its first summer (Martin et al., 1984; Baker et al., 1990), rather than by a genetically fixed behavior pattern.

Several studies indicate that maternally directed behavioral fidelity to feeding grounds has been maintained for many generations. In the North Atlantic, analysis of the amount of pigmentation on the ventral surface of flukes revealed significant differences between most feeding aggregations (Beard et al., in prep.). In the North Pacific, Baker et al. (1990) found significant differences in mitochondrial DNA haplotypes between humpback whales sampled in southeastern Alaskan waters and those sampled offshore from central California.

C. Reproduction

Reproductive parameters for humpbacks from the New England coast obtained from photo-identified individuals in the Gulf of Maine gave a crude birth rate ranging from 0.45 in 1981 to 0.103 in 1983; the same data yielded reproduc-

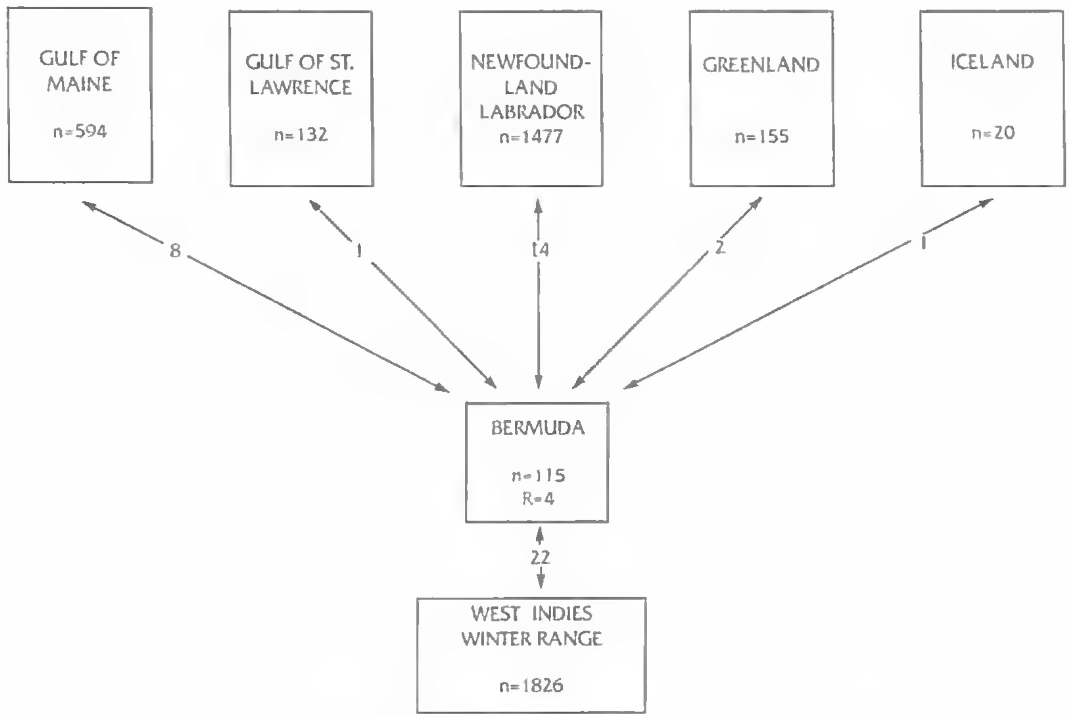

FIG. 5. Distribution of resightings of individually identified humpback whales photographed

tive rates of 0.30-0.43 calves per mature female per year (Clapham and Mayo, 1987a). Those authors and their colleagues at the Center for Coastal Studies (CCS), Provincetown, Massachusetts, now have a sample population of 97 mothers and 207 calves. The numbers of calves produced by individually identified mothers as of September, 1990, are 7 (n=1), 6 (n=3), 5 (n=5), 4 (n=6), 3 (n=14), 2 (n=22) and 1 (n=46). Nine (9) females are now grandmothers, two of them for the second time (L. Baraff, pers. comm.). As detailed by Clapham and Mayo (1987b), calves were usually born at intervals of 2 or 3 years. Two whales known from their birth year and seen annually bore calves of their own, at ages of no more than 4 years and 6 years, respectively; others with incomplete sighting histories calved at minimum ages of 5 (n=2), 6 (n=3), 7 (n=2) and 9 (n=1) years.

D. Historical Abundance

Mitchell and Reeves (1983) summarized the history of humpback whale hunting in the western North Atlantic Ocean, starting at Bermuda in 1611, Maine in 1675, Georges Bank in 1725, the Gulf of St. Lawrence in 1819, the West Indies wintering grounds in 1822, and the Canadian maritimes in the late 1800's. They accounted for at least 9,125 humpbacks killed during 1850-1971, and used their assembled catch estimates to calculate that the population size in 1865 was greater than 4,700. Breiwick et al. (1983) used the same data, but incorporated estimates for annual natural mortality (4%) and net recruitment (3%), and revised that estimate to 6,300 whales. However, many more humpback whales may have been present originally, because humpbacks had been hunted for several centuries before 1865, although catches were poorly documented (Reeves and Mitchell, 1982). Winn and Reichley (1985) listed 10,000+ as their estimate for the original population in the western North Atlantic.

Commercial hunting could have reduced the North Atlantic humpback population to as few as 700 animals by 1932 (Breiwick et al.,1983). Hunting of females with calves at locations where humpbacks returned annually for breeding probably contributed to their rapid depletion on some winter grounds Winn and Scott (1981).

No estimate of historical abundance is available for humpbacks in eastern North Atlantic waters. As reported in Reeves and Mitchell (1983), Ingebritsen (1929) calculated that 3,300 whales were killed there during 1885–1927, including 1,500 off Finnmark (central Norway) and 1,500 off Iceland. Since we now know that humpbacks from at least as far east as Iceland migrate to the West Indies and probably interbreed with the western North Atlantic stock (Mattila et al., 1989), it is unclear how Ingebritsen's data could be used to evaluate historical abundance for eastern Atlantic humpbacks.

E. Estimate of Current Abundance

Population estimates for the western North Atlantic have shown an upward trend since the 1960's, however the increase is believed to be principally due to improvements in sampling effort and methodology (Whitehead, 1987). We report here (Fig. 6) a new estimate of 5066 whales (95% confidence interval, 1800-8200), based on whales photo- identified during 1978-1988 and computed by methods detailed in Katona and Beard (1990). This represents about 80% of Breiwick et al.'s (1983) estimate for the population in 1865.

No estimate is available for current abundance of humpbacks in European waters from Iceland eastward. Luckily, Ingebritsen's (1929) statement that hunting appeared "to have entirely exterminated" the species in those waters was not correct, and studies using photo-identification and census surveys are in progress. Gunnlaugsson and Sigurjonnson (1990) used sightings from ships to estimate a population of less than 2000 humpbacks around Iceland. This was considered a great increase since protection began in 1955 and a considerable increase since the 1960's (Sigurjonsson and Gunnlaugsson, 1990). However, as shown in Sigurjonsson and Gunnlaugsson (1990), that estimate includes many sightings of humpbacks in the Denmark Strait that are probably affiliated with the western North Atlantic population, plus others sighted east of Iceland that could be from the eastern Atlantic feeding aggregation(s). Visual surveys from ships, by the Norwegian Institute for Marine Research indicated about 1,000 humpbacks in the Norwegian Sea and along the Norwegian coast in summer(Oien, 1990).

PHOTO-IDENTIFICATION AND FUTURE DIRECTIONS FOR INVESTIGATIONS ON HUMPBACK WHALES IN THE NORTH ATLANTIC OCEAN

For studying migration and population subdivisions, identification of individuals using natural markings provides the same kind of information that was previously obtained by applying artifical tags. For a species like the humpback, which possesses great individual variation in natural markings and an equally salient variety of acquired scars, each individual is marked so distinctively that artifical tags are not needed. Changes in pigmentation that occur in some individuals during early years do not compromise the accuracy of results if photo-comparisons are done carefully (Carlson et al., 1990).

Photo-identification studies do not harm target animals, are relatively inexpensive, and produce many more recaptures than did artificial tagging. For example, out of approximately 3000 humpback whales tagged with "Discovery" tags during commercial whaling or scientific studies in the Antarctic areas IV and V, 123 tags (4%) were recovered (Dawbin, 1966). The recovery rate is even lower in the western North Atlantic, where, according to Mitchell and Reeves (1983), over 160 successful implantations of Discovery tags in humpback whales produced only one significant recapture, an animal that returned to western Greenland waters in successive years (Mitchell, 1974, 1977). By comparison, the percentage of whales resighted in the same feeding aggregation during different years ranged from 5% for Iceland, which has the smallest sample size (n=20), to 62% for the Gulf of Maine, the most heavily sampled region (n=594).

The number of identified humpbacks in research collections is probably now nearly 8,000, including collections from Antarctica (50, College of the Atlantic, Stone et al., 1990, and unpublished data); Australia (600, Kaufman, 1990); Brazil (60, S. Siciliano, pers. comm.), Colombia (80, L. Flórez-González, pers. comm.), and the North Pacific Ocean (perhaps 2,500, Sally Mizroch, National Marine Mammal Laboratory, NMFS, pers. comm., including collections from Mexico, Hawaii, Japan, California, and Alaska). The amount of information on whale movements and life history will increase steadily as the number of photographs increases in future field seasons and as comparisons between regional catalogues are done.

Sophisticated cameras and film necessary for high speed, high resolution distance photography of whales did not exist during most of the period of artificial tagging, nor did the high speed boats that now bring photographers close to whales. Consequently, photo-identification studies now carried out on many cetacean species (Hammond et al., 1990) probably would not have supplanted artificial tagging much earlier than they did.

Despite its current utility, studies of humpback migration using natural markings and those using artificial marking share the weakness that only the beginning and end points of the movement are documented. Tracing migration routes will require improvements in tracking with radio tags using satellite technology (Mate, 1989).

Estimating population abundance using photo-identification is a useful, and sometimes preferable (Hammond, 1986) alternative to visual census surveys from ships or airplanes (e.g. Scott and Winn, 1980; CETAP 1982) and acoustic census surveys (e.g. Winn et al., 1975; Levenson and Leapley, 1978). Abundance estimates presented here for humpback populations of the North Atlantic and similar estimates for the North Pacific Ocean (Perry et al., 1990) are probably the most accurate available for any cetacean population over a whole ocean basin.

Nevertheless, this method can still be improved. Temporal and regional biases in sampling effort exist, and the opportunistic sampling methods usually used may bias for or against certain portions of the population (Hammond, 1986,1990). Use of a standardized sampling protocol to equalize the opportunities for all whales within a population's range to be photographed would improve the accuracy and precision of population estimates.

Data from photo-identification studies provide interesting contrasts to information from hunted specimens. Inspection of tens of thousands of carcasses allowed scientists such as Chittleborough (1958,1965) to compute mean values for life history parameters such as age, age of sexual maturity, fecundity, or growth rate. Precise as they are, such results contain two grades of uncertainty. First, they are necessarily indirect. For example, corpora albicantia, embryos or fetuses show that ovulation or pregnancy occured, but do not indicate whether a calf was born, whether it survived, or exactly how frequently reproduction occurred. Second, mean results do not describe what any real live, individual whale ever did.

Data from long term photo-identification of individuals creates the opposite problem. It can yield precise information on the reproductive rate of individuals (Glockner-Ferrari and Ferrari, 1984; Baker et al., 1986; Clapham and Mayo, 1987b, 1990) and, potentially, the survival and reproduction of their calves. However, since the large sample sizes provided by commercial whale hunting can not be obtained in a short time, statistically precise means for the population are more difficult to achieve. Nevertheless, the ability to describe the activity of a small number of real individuals offers a new perspective on the biology of the species.

A technical problem confronting large scale photo-identification studies is the increased time required for sorting large collections of photographs. It takes only a moment to read the numbers on a "Discovery" tag, and anybody can do it. Comparing photographs requires special skills: patience, attentiveness, facility at pattern-recognition and good visual memory. Only people possessing those skills should match photographs for scientific purposes. Computers get high marks for patience, attentiveness and information retention, but instructing them to find and remember a pattern is laborious. A program developed by Mizroch et al. (1990) uses videodisc storage of photographs and combines the strengths of people and computers to speed photo-comparisons. It is now used routinely in our laboratory and several others.

Use of computers will increase the rate at which photographs can be matched, reducing the number of photographs that must be checked visually, and minimizing tedium. Because it allows photographic collections to be sorted in many ways, Mizroch et al.'s (1990) system has also helped researchers to find duplicates in photographic collections. In collaboration with Sally Mizroch and the National Marine Mammal Laboratory (NMFS), we are incorporating digital analysis of images for comparison of photographs, to enhance speed and accuracy. One side benefit will be to enable researchers to compare large collections of photographs from different oceans, a project too expensive and time-consuming to be undertaken manually.

While contemplating such technological improvements, it is worth emphasizing that our eyes and brains have undergone millions of years of evolution for improved pattern recognition. These organs routinely perform complex visual operations such as translation, rotation, compensation, and decision-making that are cumbersome for even the best of today's computers. Machines will never entirely replace skilled people in analyzing individual identification photographs.

Continuing to look toward the future, challenging scientific puzzles remain to be solved for this species in the North Atlantic and other oceans. (1) During this decade, studies of migrations in the eastern North Atlantic using photo-identification will probably define the location of winter ranges and reveal the degree of separation between those animals and the western Atlantic population. (2) Precise description of migration routes for individual humpbacks is needed to provide clues about navigational mechanisms, evaluate potential energetic benefits from using wave energy to assist locomotion (Bose and Lien, 1990), facilitate detailed studies of migration and ascertain potential environmental risks to whales as they migrate through different regions. (3) Description of where, when and how copulation occurs is needed for comparison with other mating systems (Brownell and Ralls, 1986; Clutton-Brock, 1989). (4) Continued intensive regional sampling of individuals, particularly with improved sampling procedures, is needed to provide improved estimates of natality and mortality, allow construction of a life table, and reveal long term patterns of social behavior. Enough mothers need to be photographed on the winter ground with calves and then later on the summer ground to provide an estimate of calf mortality during the first six months of life. A particularly difficult, but important goal is to learn more about causes of natural mortality. The only causes specifically identified to date are killer whales (*Orcinus orca*) (Dolphin, 1987; Katona et al., 1988), sharks (Winn and Reichley, 1985; Paterson and Van Dyck, this memoir) and dinoflagellate toxins (Geraci et al., 1989). (5) Expanded use of DNA-sampling is needed to facilitate gender identification (Lambertsen et al., 1988; Baker et al., unpublished manuscript), elucidate gene flow produced by migrations (Baker et al., 1990), and contribute to interpretation of longterm matrilineal, patrilineal and social relationships.

Some of the solutions to those puzzles will not only sate our curiosity, but will allow us to respond more effectively to the overall challenge of managing humpback whales and their habitats successfully enough so that the populations recover from depletion by commercial whaling and swim the wide oceans for countless generations to come. Until Star Trek IV comes true, there is probably nothing more beneficial that we can do for this species than gather information like this and use it wisely.

It is humbling to reflect on how much of the data and how many of the future objectives presented here are merely fleshing out of the skeleton erected by previous workers, including particularly Drs. R.G. Chittleborough and W.H. Dawbin, in whose honor this conference has been organized. Everyone working on population biology, migration and reproduction is indebted to their pathbreaking research, as every list of references testifies.

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